

THE SEEDS OF THE MONSTHEREAE: THEIR MORPHOLOGY AND FOSSIL RECORD

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THE TRIBE MONSTHEREAE of the family Araceae includes some of the most magnificent and characteristic of tropical lianas. The subdivision of the tribe into genera, based largely on the placentation and septation of the ovary, has been disputed for more than a hundred years, and recent treatments indicate a continuing lack of consensus (e.g., Bakhuizen van den Brink, 1958; Bunting, 1962; and Hotta, 1970). The present paper reports the results of a study of seed morphology initiated to clarify the generic limits in this group and to account for a number of fossil seeds ascribed to one of the included genera.

Taxonomists working on the Monstereae in the past have neglected seed morphology, except for Engler and Krause (1908), who used the presence or absence of endosperm as a generic character. However, it is apparent from various erroneous illustrations that they often did not correctly interpret other features of the monsteroid seed, in particular the path of the vascular bundle in the funiculus and raphe. Our preliminary survey indicates that seed morphology is taxonomically useful at the generic or specific level in the Monstereae as well as in other tribes of the Araceae.

MATERIALS AND METHODS

This study is based primarily on specimens of about 70 species in the herbaria of the Arnold Arboretum (A) and the Gray Herbarium (GH) of Harvard University; additional reports in the literature bring the total number of species investigated to about 80. This number is approximate, because the tribe is sorely in need of revision and the specific identification of specimens is often doubtful. Developmental studies in *Rhodospatha* and *Monstera* are based on material collected in the wild and preserved in formalin-acetic-alcohol (voucher specimens in GH). Developmental studies in other genera are based on rehydrated herbarium material. Published illustrations of the fossils have been examined, but not the fossils themselves.

MODERN SEEDS

In the seeds of the Monstereae there is a correlation between size, curvature, and relative abundance of endosperm. The range includes small uncurved seeds with relatively abundant endosperm to large highly curved seeds lacking endosperm. In this series six morphologically distinct types

of seeds may be recognized. Each genus accepted by Engler and Krause (1908) is constant for one of these types, but their genera are not all separable by this character alone.

Seeds of a number of extant species are illustrated in FIGURES 1 to 47; the letters c, h, m, and r in FIGURES 1 to 6 refer respectively to the chalaza, hilum, micropyle, and raphe. The term "ventral face" is here applied to the side of the seed bearing the raphe, which faces the placenta or the axis, while the "dorsal face" is directed either upward or outward.

Stenospermation Schott (FIGURES 1, 8, 9) is a neotropical genus of about 20 species characterized by smooth, anatropous, subterete seeds 2–2.5 mm. long and 1 mm. in diameter. The seeds are flattened on the ventral (raphal) surface and slightly dorsally inflated toward the chalazal end. The adnate funiculus forms a ventral raphe visible as a dark line leading to the chalazal end; the micropyle is dorsal to the hilum on the flattened nucellar end. In the development of the seed the anatropous ovule elongates but does not become curved. The embryo is straight and fusiform, surrounded by abundant endosperm.

Rhaphidophora Hassk. (FIGURES 2, 10–20) includes about 60 species occurring in West Africa, from Indomalesia to Samoa, and north to Formosa. The seeds are smooth, anatropous, subterete to ellipsoid, 1–3 mm. long, and 0.5–1 mm. thick. The subterete specimens have a flattened raphe-bearing ventral face similar to that of *Stenospermation*. In the ellipsoidal forms (FIGURES 10, 14, 17), the ventral face is not flattened. In general the seeds of *Rhaphidophora* are very similar to those of *Stenospermation*. In both of these genera the small size of the seeds is clearly related to the large number of seeds per ovary, but even in those specimens which set only a few seeds per fruit, the size and morphology of the seeds remain characteristic of the genus.

Epipremnum Schott (FIGURES 3, 21–25) includes about 15 species ranging from Indomalesia to Samoa and the Marshall Islands. The seeds are symmetrically to asymmetrically reniform, 3–7 mm. long, and 1.5–4 mm. across. The raphe passes from the hilum to the slightly inflated chalazal end along the concave ventral surface, often producing a chalazal ostiole where it penetrates the testa. The micropyle, occasionally represented by a small black hole (as in FIGURE 3), is situated on the inner margin of the nucellar end dorsal to the hilum. The surface morphology varies from smooth (FIGURES 22, 24) to rugose (FIGURES 21, 25). In *E. pinnatum* (FIGURE 23) the surface often but not always bears pits in the hard seed coat; these and the epidermal cells of the testa are arranged in parallel rows following the curvature of the seed axis. The curved embryo is embedded in endosperm.

Rhodospatha Poepp. & Endl. (FIGURES 4, 26, 27) comprises about 15 species of the neotropical mainland. The seeds are anatropous, reni-

form to cordiform in outline and terete to slightly flattened in cross section, 1–1.5 mm. wide, and about 0.5 mm. thick. The fine black raphe passes from the narrowed and occasionally stalklike hilar end along the strongly concave ventral face to the slightly inflated chalazal end (FIGURE 27); the chalaza appears as a black spot in specimens divested of their outer testal layer. The micropyle is dorsal to the hilum on the nucellar end. The dorsal margin of the seed is cristate, and in material preserved in FAA it exhibits radiating processes extending 1–2 mm. beyond the seed surface. During development of the seed, the ovule bends about the raphe, giving rise to the curved condition of the mature seed.

Scindapsus Schott (FIGURES 5, 28–34) includes about 25 species ranging from India and Sikkim to the Solomon Islands and one species in South America. The anatropous seeds, 3–9 mm. long and 2–5 mm. wide, vary in outline from broadly reniform (FIGURES 20, 30) to cordiform, with those of *S. officinalis* almost horseshoe-shaped, the enclosed ventrally directed space being covered by a membrane (FIGURE 31). In cross section the seeds are round to ellipsoidal. The raphe passes along the concave ventral surface from the hilum to the chalazal end, which in some species (FIGURES 28, 30, 32) is longer than the nucellar end. In *S. officinalis* (FIGURES 5, 31) the hilum is marked by an irregularly bordered scar which overlies the chalazal end. The micropyle is dorsal to the hilum and is subtended dorsally by a thickened ridge. The outer surface is smooth (FIGURES 30, 32, 33) or faintly radially striate (FIGURES 28, 29, 31, 34). The developing seed is initially straight, but it curves around the raphe as it grows. The embryo is macropodial and endosperm is lacking.

Monstera Adanson (FIGURES 6, 7, 35–44), a neotropical genus of about 25 species, has oblong-ellipsoidal to subglobose seeds 6–18 mm. long and 4–12 mm. wide. The morphology of these seeds is best understood by considering their ontogeny, as illustrated by *M. dubia* (FIGURE 7). The developing anatropous ovule is initially only slightly curved, but in growth it reflexes about the funiculus, thereby causing the raphe to follow an S-shaped course in the mature seed. The hilum appears either as a small stalk (FIGURES 6, 7, 42) or as a depressed channel (FIGURES 35, 37–40, 43, 44). The micropyle is on the opposite side of the hilum from the chalaza. The ontogeny of the seeds of most species is culminated by growth in the dorsal direction, yielding a dorsoventrally elongate shape. The smooth surface of the seed is frequently marked by numerous light-colored raphide sacs embedded in the soft testa. The embryo is macropodial and endosperm is absent.

Amydrium Schott (FIGURE 45) comprises four species of Thailand and Malesia. In *A. magnificum* the seeds are subglobose to subreniform in outline and approximately 7 mm. long by 9 mm. wide. In the ovule the raphe curves well around the chalazal end, and with later growth

both the chalazal and nucellar ends enlarge considerably and bend ventrally. In the mature seed the funiculus has become adnate to the testa about one third of the way from the nucellar end, and the raphe arches away from the seed above the ventral concavity before entering the chalaza. The seed coat is smooth and is marked by light-colored raphide sacs. The embryo is macropodial and endosperm is lacking. Nicolson (1968) considered this genus to be close to *Epipremnum*, but the limited material at our disposal suggests that its seed morphology is closer to that of *Monstera*. In *Amydrium*, however, most of the seed elongation is lateral rather than dorsal, with the consequence that the raphe is shallowly instead of sharply S-shaped.

FOSSIL SEEDS

Tertiary carpological remains attributed to the Monstereae include three genera and twelve species of seeds and spadices. These range in age from the lower Eocene to the Pliocene and geographically from western Europe through Central Asia, with one specimen reported from the southeastern United States. Comparison of these fossils with modern forms suggests that only four species are assignable to the Monstereae. One fossil may be referred to *Anadendrum* of the subfamily Pothoideae, three more are assignable to the subfamily Lasioideae, and the remaining species are of uncertain affinity. The necessity of comparing published illustrations of these fossils with the modern seeds constrains us to suggest affinities rather than to propose a formal taxonomic revision of the fossil material, although such a revision seems appropriate in many cases. This cautious attitude is reinforced by the possibility of unrecognized similar seed morphologies in groups unrelated to the Araceae. Kirchheimer (1957) has noted the similarity of seeds of *Epipremnum* to those of species of the Leguminosae and Malvaceae.

The identification of the fossils is based on their morphological similarity to modern forms and on the climatic affinities of the floras associated with the fossils. The extant Monstereae are primarily tropical. The association of a putative fossil *Epipremnum* with a pronouncedly temperate flora, particularly when coupled with an inappropriate morphology, suggests the rejection of such a form from the Monstereae. In several cases individual citations within a species are questioned without implying the potential rejection of that species.

SPECIES ASSIGNABLE TO THE MONSTEREAE

Epipremnum crassum C. & E. M. Reid, Pliocene floras of the Dutch-Prussian border. 71. *pl.* 4, *figs.* 1-9. 1915. [Pleistocene].

DOROFEEV, P. I., *Voprosy Geol. Vost. Okr. Russk. Platf. Yuzhn. Urala* 5, Bashk. Fil. Akad. Nauk SSSR. 18. *pl.* 3, *figs.* 3, 4. 1960. [Pliocene]; *Dokl. Akad. Nauk SSSR*, 144: 650. *pl.* 1, *figs.* 14, 15. 1962. [Miocene]; *Problemy*

- Botaniki 6: 50. *pl.* 2, *fig.* 3. 1962. [Miocene?]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 133. *pl.* 16, *figs.* 13–16. 1963. [Miocene?]; Bot. Zhur. 51: 1481. 1966. [Miocene]; Miotsenovaya flora Mamontovoi Gary Na Aldane. [The Miocene flora of the Mammoth Mountain on the Aldan River.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 57. *text fig.* 12; *pl.* 8, *figs.* 1–5. 1969. [Miocene]; Tretichnye flory Basseina r. Omoloya. [Tertiary flora from Basseina on the River Omoloya.] Akad. Nauk SSSR. Vsesoyuznoe Botanicheskoe Obshchestvo. 82. *pl.* 8, *figs.* 7, 8. 1972. [Tertiary].
- NIKITIN, P. A., Compt. Rend. Acad. Sci. URSS 3: 134. 1935. [Miocene–Pliocene]; The Pliocene and Quaternary floras of the Voronezh region. Izdat. Akad. Nauk SSSR. 123. *pl.* 3, *figs.* 33–37. 1957. [Pliocene].
- REID, E. M., Bull. Soc. Géol. France IV. 20: 63. *pl.* 3, *figs.* 13, 15. 1920. [Pliocene]; *Ibid.* 23: 315. 1923. [Pliocene].
- VLERK, I. M. VAN DER, & F. FLORSCHÜTZ, Nederland in het Ijstijdvak. 76. *fig.* 20. 1950. [Pleistocene].

Anatropous seed, about 3 mm. long and 2.5 mm. wide, reniform, reflexed approximately 120° – 180° ; chalazal and nucellar ends of equal length, both rounded, the ventral hollow frequently covered so that the ventral face appears almost flat (with the exception of that figured by Dorofeev, 1969), the ventral face occasionally with a conspicuous round protuberance; surface of the seed smooth to faintly pitted, perhaps from raphide sacs.

The specimens of the fossil are morphologically similar to *Epipremnum*, but they exhibit considerable variability, suggesting that the concept of the fossil may encompass more than one species. In addition, the associated floras range from marginally subtropical to interglacial, suggesting that some of the citations may not refer to seeds of Monstereae. The type specimen and the specimens described by Dorofeev (1962b, 1963) possess a small but prominent ventral protuberance, a feature not seen in any other fossil or modern Monstereae. However, Dorofeev (1963) illustrated four seeds which apparently intergrade from forms possessing this protuberance (FIGURE 16) to those lacking it (FIGURE 14). The significance of this character remains unclear. Dorofeev (1969) illustrated in his *text fig.* 12 four forms, of which the one on the lower left is possibly an aroid seed. The remaining three, as well as those illustrated by Dorofeev (1960, *fig.* 4) and Van der Vlerk and Florschütz (1951), are distinct from any monsteroïd or lasioïd seed seen by us in their deeply rounded shape and often flat, multiperforated ventral face and should be excluded from the Araceae. The morphology of the remaining seeds attributed to this species is best illustrated by Dorofeev (1962a) but is too indistinct to permit certain referral to an extant species. These seeds are most probably allied with the modern genera *Epipremnum* and *Scindapsus*.

It is doubtful that *Epipremnum* could survive the rigors of a European glacial period by migrating over the Alpine system, and the speci-

mens described by Reid and Reid (1915) and Van der Vlerk and Florschütz (1951), already considered dubious on morphological grounds, are of interglacial age. Dorofeev (1960) and Nikitin (1957) described *E. crassum* from deposits particularly poor in thermophilic East Asian elements, suggesting that these specimens, although morphologically acceptable, are also suspect. The remaining floras, although not tropical, are warm-temperate to marginally subtropical and are conceivably capable of supporting *Epipremnum*.

Epipremnum ornatum E. M. Reid & M. E. J. Chandler, The Bembridge flora. Brit. Mus. Nat. Hist. 83. *pl.* 4, *figs.* 24, 25. 1926. [Oligocene].

Epipremnum ornatum Reid & Chandler.

DOROFEEV, P. I., Dokl. Akad. Nauk SSSR. 101: 941. *pl.* 1, *figs.* 5, 6. 1955. [Tertiary]; Sbornik Pamy. A. N. Krystofovich, Akad. Nauk SSSR. Bot. Inst. V. L. Komarova. 301. *tab.* 2, *figs.* 17-19. 1957. [Tertiary]; Dokl. Akad. Nauk SSSR. 123: 173. 1958. [Oligocene]; *Ibid.* 123: 543. 1958. [Oligocene]; *Ibid.* 127: 1104. 1959. [Oligocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 131. *pl.* 16, *figs.* 17-21. 1963. [Tertiary]; Bot. Zhur. 51: 1481. *pl.* 1, *fig.* 42. 1966. [Miocene]; Tretichnye flory Basseina r. Omoloya. [Tertiary flora from Basseina on the River Omoloya.] Akad. Nauk SSSR., Vsesoyuznoe Botanicheskoe Obshchestvo. *pl.* 8, *fig.* 9. 1972. [Tertiary].

KOLESNIKOVA, T. D., Bot. Zhur. 45: 118. *pl.* 1, *fig.* 2. 1960. [Miocene]; *Ibid.* 46: 126. *pl.* 1, *fig.* 4. 1961. [Miocene].

NIKITIN, P. I., Akvitanskaya Semennaya flora Lagernogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 63. *pl.* 7, *figs.* 5-9. 1965. [Tertiary].

Rhaphidophora ornata (Reid & Chandler) Chandler, Bull. Brit. Mus. Nat. Hist. Geol. 6(3): 364. 1963. [Oligocene].

Anatropous seed, 2-3 mm. long, approximately 2.2 mm. wide, reniform, reflexed 90°-160°; tapered nucellar end truncate and in lateral view longer than the rounded chalazal end; seed surface smooth.

These small, smooth seeds appear in both size and shape to belong to one species, although the illustrated type (Reid & Chandler, 1926) is a particularly poor specimen. The morphology and the frequent presence of small pits (perhaps indicative of raphide sacs) place this form, in our opinion, close to the extant species *Epipremnum pinnatum* of southeastern Asia and Oceania. Chandler (1963) places these fossils in the genus *Rhaphidophora*, remarking that "the uniform spongy equiaxial cells throughout the testa in the species are not fully in accord with the structure of *Epipremnum* as shown by Kirchheimer (1957, *pl.* 12, *fig.* 54a) and it seems probable that these seeds should be referred to the related genus *Rhaphidophora* (Dorofeev ex lit. 9.5.59)." Though the anatomy of these fossils may be at variance with that of modern *E. pinnatum*, their external morphology definitely excludes them from the genus

Rhaphidophora. This anatomical difference may arise from ecotypic variation or evolutionary modification, or it may represent a species-level distinction. With the exception of that reported by Kolesnikova (1960), the floras associated with this species are of a subtropical to warm-temperate East Asian affinity. While these floras do not entirely support the identification of the species, they do not disqualify it either.

Epipremnum uralense P. I. Dorofeev, Dokl. Akad. Nauk SSSR. 168: 685. *pl.* 1, *figs.* 1-3. 1966. [Oligocene]; Paleontol. Zhur. 2: 248. *pl.* 17, *figs.* 9, 10. 1968. [Oligocene]; Tretichnye flory Urala. [The Tertiary floras of the Ural.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 34. *pl.* 5, *figs.* 4-6. 1970. [Oligocene].

Anatropous seed, 2×2 mm., reniform, reflexed 140° - 180° ; nucellar end tapered and truncate, the chalazal end broadly rounded, and in lateral view the nucellar end longer than the chalazal end; surface smooth or pitted.

The morphology of this seed is close to that of *Scindapsus*, particularly *S. rupestris* (FIGURE 32). No further data are available to support this similarity, and the fossil might easily represent a separate or extinct species. The associated floras reflect a warm-temperate East Asian aspect, and (especially in Dorofeev, 1970) they may represent a mountainous flora within a generally warmer climate not unlike that of the present lower slopes of the Himalayas. The Mid to Late Oligocene has been interpreted as a period of expansion of the paleotropical elements of the European Tertiary, and it is not inappropriate to find members of the Monstereae in this type of flora.

Epipremnum species C. & E. M. Reid, Pliocene floras of the Dutch-Prussian border. 72. *pl.* 4, *figs.* 13, 14. 1915. [Pleistocene].

Anatropous seed, 1.3 mm. long, 2.2 mm. wide, reniform, reflexed 140° - 180° ; chalazal and nucellar ends of equal length, rounded; smooth surface faintly pitted, indicating raphide sacs.

With the exception of its smaller size, this fossil is an exact replica of the seed of *Epipremnum pinnatum* of the modern flora, but its presence in an interglacial deposit (Van der Hammen, 1951) makes it highly suspect. We retain it in this section of the discussion solely on the basis of the striking morphological similarity, but we suggest that it represents an unrecognized form masquerading as a monsteroid seed.

SPECIES ASSIGNABLE TO THE POTHOIDEAE

Araceites hungaricus K. Rásky, Ann. Hist.-Nat. Mus. Hungar. 56: 70. *pl.* 9, *fig.* 5. 1964. [Oligocene].

This well-preserved impression is a 2.5 cm. long and 1.2 cm. wide frag-

ment of a spadix possessing perfect flowers with a large central stigmatic region enclosed by a fused and reduced perianth. These characters suggest the Asian genus *Anadendrum*, to which fossil remains should perhaps be referred. *Anadendrum* is intermediate between the subfamilies Monsteroideae and Pothoideae, and, although Hutchinson (1959) referred it to the Monstereae, we follow Engler and Krause (1908) in referring it to the Pothoideae. The associated flora is subtropical and supports the generic assignment.

SPECIES ASSIGNABLE TO THE LASIOIDEAE

Epipremnum cristatum P. A. Nikitin, Akvitanskaya flora Lagernogo Sada 7: 11–14. 1944. [not seen; cited by Dorofeev, 1952]; Akvitanskaya Semennaya flora Lagernogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 64. *pl.* 7, *figs.* 10–14. 1965. [Tertiary].

Epipremnum cristatum Nikitin.

BŮŽEK, Č., & R. HOLÝ, Sborn. Geol. Paleontol. 4: 126. *pl.* 6, *figs.* 10–13. 1964. [Miocene].

DOROFEEV, P. I., Bot. Zhur. 37: 854. *pl.* 2, *figs.* 13, 14. 1952. [Pliocene]; Dokl. Akad. Nauk SSSR. 123: 173. *pl.* 1, *fig.* 8. 1958. [Oligocene]; *Ibid.* 127: 1104. 1959. [Oligocene]; *Ibid.* 144: 650. 1962. [Miocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Siberia.] Izdat. Akad. Nauk SSSR. 132. *pl.* 16, *figs.* 9–12. 1963. [Tertiary]; Bot. Zhur. 51: 1481. *pl.* 1, *fig.* 43. 1966. [Miocene].

KOLESNIKOVA, T. D., Bot. Zhur. 45: 119. *pl.* 1, *fig.* 3. 1960. [Miocene]; *Ibid.* 46: 126. *pl.* 1, *fig.* 3. 1961. [Tertiary].

PALAMAREV, E., Bulgar. Akad. Wiss. Mitt. Bot. Inst. 20: 61. *pl.* 6, *fig.* 15; *pl.* 7, *fig.* 1. 1970. [Miocene-Pliocene].

SZAFER, W., Instyt. Geol. Prace. 33: 93. *pl.* 25, *figs.* 3–5. 1961. [Miocene].

Carpolithus cristatus (Nikitin) D. H. Mai, Paläontol. Abhandl. B. 2: 53. *text fig.* 10; *pl.* 4, *figs.* 24, 25; *pl.* 6, *fig.* 12. 1964. [Miocene].

Anatropous seed, 2.5–3.5 mm. long, 1.5–2.5 mm. wide, reniform, reflexed 90°–140°; chalazal end lower than the nucellar end in lateral view, the nucellar end flattened, the chalazal end tapered, both ends often bearing spines; dorsal and lateral faces bearing parallel ridges capped with strongly protuberant spines.

These distinctively spinose seeds are widely reported from the Tertiary of Europe and western Asia. With the exception of those illustrated by Palamarev, all of the figured forms definitely belong to the same specific entity. The seeds of *Epipremnum cristatum* do not resemble those of any extant species in the genus *Epipremnum* or those of any other monsteroide form seen by us. The prominent parallel rows of dorsal tubercles and the wide, flattened nucellar end are shared with a number of genera in the subfamily Lasioideae of the Araceae, including *Dracontioides*, *Dracontium*, and *Cyrtosperma*. Dorofeev (1963) has noted that *E. cristatum*

is only nominally assigned to *Epipremnum* and probably conforms more closely to *Cyrtosperma*. The exact disposition of *E. cristatum*, as with the following two species, must await an investigation of the seeds of the Lasioideae. The seed illustrated by Mai (1964) conforms to the morphology of *Epipremnum cristatum*, although he has labeled what is probably the chalazal end as the hilum.

The associated floras exhibit subtropical to warm-temperate affinities, with the exception of the flora described by Dorofeev (1952), which is cool-temperate. Although the Lasioideae are primarily tropical, some genera (e.g., *Amorphophallus*) extend as far north as Japan. The possible derivation of the forms of the European Tertiary from these northern species should not be overlooked.

Epipremnum rugosum P. I. Dorofeev, Dokl. Akad. Nauk SSSR. 137: 924. *pl.* 1, *fig.* 18. 1961. [Oligocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 132. *pl.* 16, *figs.* 1-8. 1963. [Tertiary].

Anatropous seed, approximately 3.8×3.5 mm., irregularly reniform; nucellar end flattened, the chalazal end tapered, and the two ends of approximately the same length in lateral view; dorsal surface showing numerous low, irregularly distributed small to large diameter tubercles.

The parallel rows of dorsal rugosities and the flattened nucellar end place the fossil in the subfamily Lasioideae, and Dorofeev (1963, p. 132) has noted that "this species is close to *Epipremnum cristatum* Nikitin, but it is undoubtedly independent. Perhaps it is another genus, for example, *Cyrtosperma*." This determination is only weakly supported by the warm-temperate, partly East Asian affinities of the associated floras.

Epipremnum visimense P. I. Dorofeev, Tretichnye flory Urala. [The Tertiary floras of the Ural.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 35. *text fig.* 2; *pl.* 5, *figs.* 1-3. 1970. [Oligocene].

Anatropous seed, about 2×2 mm., irregularly reniform, reflexed about 90° ; nucellar end longer than the chalazal end in lateral view, the nucellar end flat, the chalazal end broadly rounded; two(?) low dorsal and two low dorsolateral mildly serrate ridges appearing as the only gross sculpture.

The affinities of this species lie with the subfamily Lasioideae, as indicated by the parallel dorsal and dorsolateral ridges and the broadly flattened nucellar end. Dorofeev (1970, p. 36) notes that the seed is only provisionally attributed to *Epipremnum* and is probably closer to *Cyrtosperma*. *Epipremnum visimense* is distinguished from *E. rugosum* and *E. cristatum* by its neatly parallel rows of low dorsal protuberances, in contrast to the unevenly distributed dorsal protuberances and larger size of

E. rugosum and the parallel but longer dorsal spines of *E. cristatum*. The presumed affinities of this seed with the Lasioideae are compatible with the warm-temperate to subtropical East Asian nature of the fossil floras with which it is associated.

SPECIES OF UNCERTAIN AFFINITY

Araceaeites parisiensis P. H. Fritel, Mém. Soc. Géol. France Paléontol. 40: 28. text. fig. 15; pl. 3, fig. 1. 1910. [Eocene].

Araceaeites fritelii E. W. Berry, U. S. Geol. Surv. Prof. Paper 91: 175. pl. 114, figs. 3, 4. 1916. [Eocene].

The genus *Araceaeites* was proposed for fossil spadices of Araceae and includes material of diverse affinities. We have already noted the similarity of *A. hungaricus* to the extant genus *Anadendrum*. The small (46 × 6 mm.) spadix of *A. parisiensis* figured by Fritel is compared by him to that of the modern genus *Spathiphyllum*. Though he mentions and figures what is probably the stigma of each flower, no mention is made of a possible perianth. The small size suggests *Spathiphyllum* or *Rhaphidophora* or even *Monstera*. Though apparently in the Araceae, the exact affinities of this specimen remain obscure. *Araceaeites parisiensis* is from the Lower Eocene of the Paris Basin and is associated with a strongly subtropical to tropical flora with East Asian affinities.

Araceaeites fritelii of the Eocene of the southeastern United States is so poorly preserved that it defies identification on the basis of published illustrations at ranks below the family level. The climate of the Eocene of the southeastern United States is characterized by Dilcher (1971, p. 18) as a "seasonally dry to slightly moist moisture regime and an equable warm temperate to cool subtropical temperature regime."

Acoropsis minor H. Conwentz, Die Flora des Bernsteins, II. Die Angiospermen des Bernsteins. 12. pl. 1, figs. 14-17. 1886. [Eocene].

Carex eximia Goeppert & Menge, Monatsber. Königl. Akad. der Wissenschaften Berlin. 459. 1853. [Eocene].

This fructification has been variously referred to *Carex* (Goeppert & Menge, 1853), *Acorus* (Araceae, Pothoideae; Conwentz, 1886), and the Monstereae (Bogner, pers. comm.). Kirchheimer (1957) felt that it lacked sufficiently distinctive characteristics to warrant identification, but examination of the illustrated material does suggest affinity with the Monstereae. The reader is referred to Bogner's forthcoming paper (in manuscript).

Cyrtospermites hordwellensis (Chandler) Bogner, Taxon 22: 321. 1973.

Campylopermum hordwellensis M. E. J. Chandler, The Upper Eocene flora of Hordle, Hants, I & II. Palaeontographical Soc. London. 16. *text. fig. 4; pl. 1, fig. 6a-c.* 1925 & 1926. [Eocene].

A seven(?)-seeded, thin-walled berry, with parietal placentation according to Chandler, $4 \times 3.5-5$ mm., the seeds 4×2 mm., reflexed approximately 180° ; nucellar end longer than the chalazal end in lateral view, both rounded; surface of the seed obscured by the berry, but the raphal path on the arcuate ventral face clear.

This several-seeded berry was initially described as the fossil genus *Campylopermum*, which is a later homonym of a genus in the Ochnaceae. The required new name was supplied by Bogner in 1973. The form of the seed suggests that the species belongs to the Monsteroideae or Lasioideae, but the available characteristics do not allow any further distinctions. The affinity implied by the name *Cyrtospermites* is unfortunate, since the seeds possess no characteristic that definitely links them to the modern genus *Cyrtosperma*. The associated flora is tropical to subtropical, with strong East Asian affinities.

Epipremnum reniculum (Ludwig) F. Kirchheimer, Bot. Jahrb. 67: 79. *pl. 11, fig. 33a-i.* 1935. [Oligocene].

Epipremnum reniculum (Ludwig) F. Kirchheimer.

DOROFEEV, P. I., Bot. Zhur. 45: 1419. *pl. 3, figs. 5, 6.* 1960. [Oligocene]; Nizhniĭ Pleistotsen Lednikovykh Raionov Russkoĭ Ravniny. Akad. Nauk SSSR. Kom. po Izuch. Chetvertichnogo Perioda. *pl. 2, figs. 13, 14.* 1967. [Pleistocene].

Cytisus reniculus Ludwig, Palaeontographica B. 5: 101. *pl. 20, fig. 21.* 1857. [Pliocene].

Carpolithus reniculus (Ludwig) P. Menzel, Jahrb. Preussisch. Geol. Landesanstalt 34: 19. *pl. 1, fig. 37.* 1913. [Oligocene].

KIRCHHEIMER, F., Das Hauptbraunkohlenlager der Wetterau. 36. *pl. 9, figs. 7-10.* 1934. [Pliocene]; Die Laubgewächse der Braunkohlenzeit. 113, 348. *pl. 12, figs. 53, 54.* 1957. [Oligocene].

MAI, D. H., Paläontol. Abhandl. B. 2: 53. *pl. 4, figs. 26, 27.* 1964. [Miocene].

Carpolithus reniformis V. Fritsch, Jahrb. Preussisch. Geol. Landesanstalt 5: 437. *pl. 26, fig. 26.* 1884. [Pliocene].

Anatropous seed, 2.5 mm. long, 1.5-2 mm. wide, reniform to cordate, reflexed $120^\circ-160^\circ$, the ventral hollow small or lacking, giving the seed a rounded appearance, the round to slightly flattened nucellar end as long as the round to tapered chalazal end in lateral view; surface smooth.

The systematic placement of this species is uncertain. Although Dorofeev (1960) accepted it as *Epipremnum*, Kirchheimer (1957) referred it to the form genus *Carpolithus*, noting its strong resemblance to the seeds of *Kitaibelia vitifolia* (Malvaceae) and *Cytisus* (Leguminosae). Simul-

taneously he enlarged the species concept to include the fossils described as *E. crassum* Reid & Reid.

The size, general outline, prominent micropyle, and external pitting of many of these fossils does suggest *Epipremnum*, but the fossils do not closely match the seeds of any extant species. Those illustrated by Mai (1964) are interpreted by him as possessing a micropyle and hilum on opposite ends of the seed; if this is correct, the fossil is definitely excluded from the Monstereae. Kirchheimer's (1957) sections of modern *Epipremnum pinnatum* reveal a thin-walled testa composed of elongate sclereids, whereas the fossil possesses a thick testa of isodiametric ones.

The floras accompanying these fossils range from subtropical to interglacial. The anatomical distinctions and the varied climatic relations of this species suggest that few, if any, of its assigned members belong to the Araceae.

Epipremnum sp. 3? P. A. Nikitin, Akvitanskaya Semennaya flora Lager-nogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 65. *pl.* 7, *fig.* 15. 1965. [Tertiary].

This small (1.62×1.04 mm.) seed is the wrong shape to be that of a modern *Epipremnum*, and it possesses a medial perforation not seen in the seeds of any of the modern species. It may be excluded from the genus and perhaps from the family.

Aracispermum Nikitin.

A genus comprising at least six species, with ovoid to elongate-ovoid orthotropous seeds ranging from 1 to 4 mm. in length and 1 to 2 mm. in diameter; seeds externally smooth or longitudinally furrowed, the base rounded to pointed and the apex with a conical depression leading to an internal cavity.

Mai (1964) observed that the characters of these seeds, particularly of the central cavity and the apical "micropylar canal," suggest the families Araceae or Zingiberaceae. However, both he and Lańcucka-Środoniowa (1966) note that no comparable modern genus is known. We cannot offer suggestions as to the identity of these seeds, but they can definitely be excluded from the Monstereae.

DISCUSSION

In the Monstereae there is a correlation of seed size, seed curvature, and relative abundance of endosperm, ranging from small uncurved seeds with abundant endosperm to large, highly curved seeds lacking endosperm. These seem to represent a simple allometric series, although the seeds of *Rhodospatha* are somewhat smaller than would be expected for their degree of curvature in the context of the tribe as a whole, and those

of *Amydrium* are somewhat larger. The extant genera occupy discrete intervals in this series, and seed morphology is a useful generic character, particularly in separating *Rhaphidophora*, *Epipremnum*, and *Monstera*, many species of which are very similar in other respects.

The curvature of the seeds appears to be a consequence of the slower growth of the funiculus and raphe in relation to the elongation of the rest of the seed. Large *Monstera* seeds require a year to develop; it is not surprising that the heavily vascularized raphe cannot continually elongate during that time. The static length of the raphe coupled with the continuing growth of the rest of the seed in the confines of a narrow ovary necessarily results in curvature of the seed about the raphe.

The presence or absence of endosperm in the mature seed seems to depend on the relative growth rates of the embryo and endosperm. In large seeds the relatively faster growing embryo consumes the endosperm by maturity, whereas in smaller seeds the embryo growth rate is slower and maturity is achieved prior to the consumption of the endosperm. In the developing *Monstera* seed the endosperm is initially dominant, but the developing embryo soon consumes the endosperm at a more rapid rate than it is produced. By the time the seed has become curved, but prior to the initiation of dorsal elongation, the endosperm constitutes about one fifth of the volume of the seed. This remaining endosperm is consumed during the final dorsal elongation. The possibility of a neotonic derivation of *Epipremnum*-like forms from *Monstera* must be discounted. In *Epipremnum* the embryo is axile and surrounded by a sheath of endosperm, whereas in *Monstera* all of the endosperm at the nucellar end is consumed during the early stages of growth and the embryo then contacts the endosperm on only one face as the seed curves and enlarges.

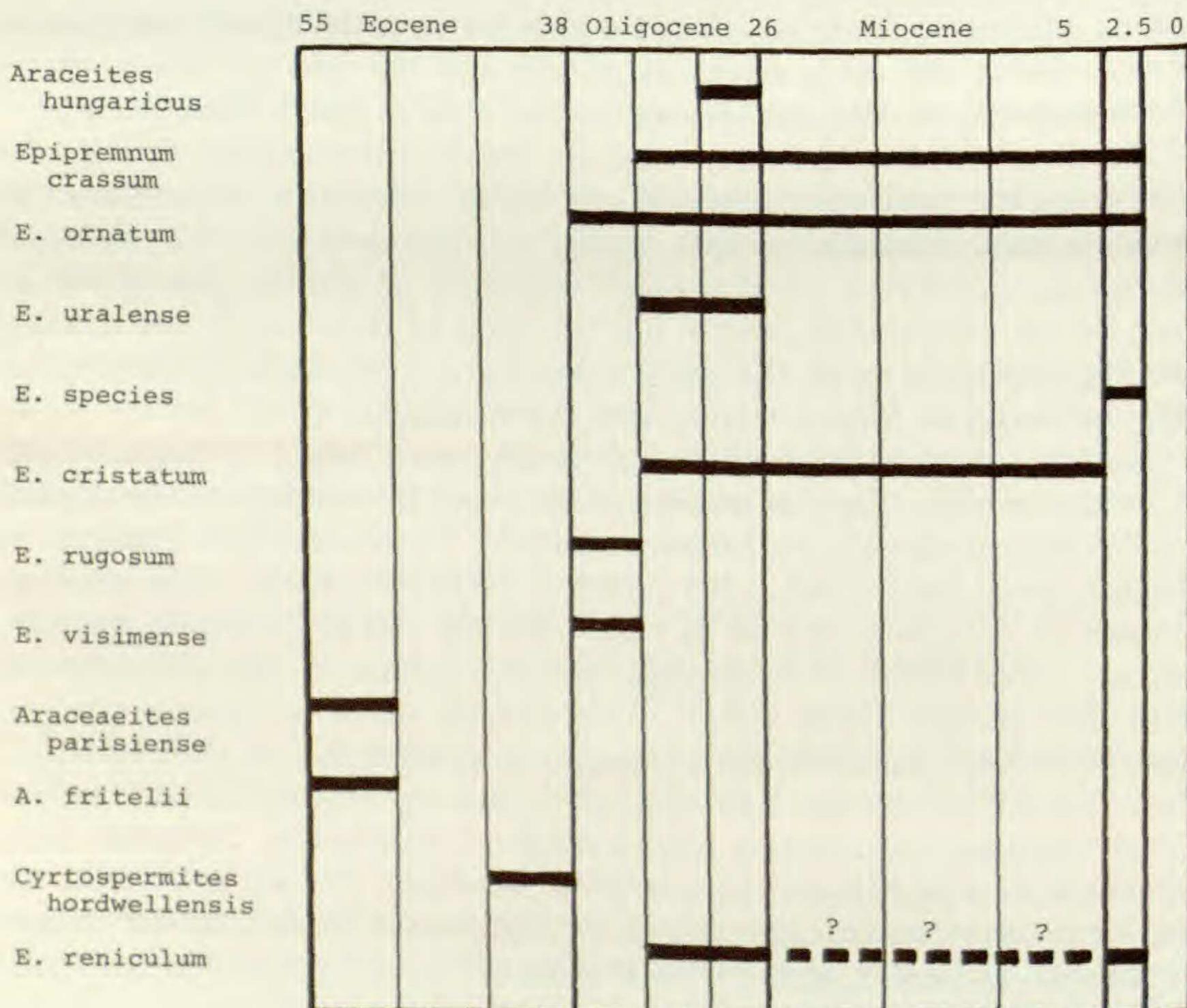
The fossil seeds which we accept as *Epipremnum* readily fit into the morphological sequence evident in the extant species of Monstereae. In addition, they resemble modern species of *Epipremnum* in the pitting of the surface. However, the associated vegetative or fruiting remains necessary for an unequivocal generic identification of these fossils are lacking, and the possibility exists that some modern group unrelated to the Araceae may be found to have a similar seed morphology.

The considerable geographic and stratigraphic range of these fossils is worthy of note. The low number of described Eocene Araceae is surprising in view of the known Eocene maximum of paleotropical elements in the European flora (Mai, 1965; Reid & Chandler, 1933). The greatest number of coexisting species of fossil Araceae (seven) occur in the Oligocene, concomitant with the last major advance of the paleotropical flora into Europe (Mai, 1965). This number drops to three species at the Oligocene-Miocene border with the commencement of the retreat of the thermophilic floras. The "warm temperate, subtropical and rather humid" climate suggested by Schwarzbach (1966) for the European Late Oligocene to Mid Miocene gave way to increasing cooling and aridity in the Late Miocene and Pliocene, presumably causing the retreat or extinction of tropical Araceae from Europe.

The present-day distribution of the Monstereae is primarily neotropical and Indomalaysian, with two species in West Africa, and it ranges from 27° south latitude to 28° north latitude. The most nearly extratropical members of the tribe are *Rhaphidophora* and *Scindapsus*, which ascend to 2000 m. in the Himalayas, and *Monstera*, which in northern Central America occurs in cool forests at 2500 m. *Monstera deliciosa* persists in subtropical Florida, although it is not native there. The floras associated with the fossil Monstereae range from tropical and subtropical to warm-temperate. While these floras are not altogether incompatible with the ecological tolerances of modern Monstereae, they suggest that some of the fossilized forms may represent individuals at the edge of their range. It is also conceivable that extinct Monstereae had a wider ecological amplitude than modern species.

Engler and Krause (1908) proposed that the neotropical Monstereae were derived from the paleotropical forms. The existence of seeds of this tribe in European and Siberian Tertiary deposits as far as 50° to 55° north latitude suggests that the group once had a more cosmopolitan distribution than at present. The paucity of reported New World fossil material may reflect less intensive sampling or the absence of the family in the Paleogene of the New World. If future work reveals North American fossil material,

TABLE 1. Distribution of the fruiting remains of the Araceae (excluding *Aracispermum Nikitin*) in the fossil record. Time in millions of years.



then the similarities of the African and South American forms could be ascribed to a common derivation from a Paleogene Boreotropical flora, in keeping with Wolfe's (1975) hypothesis. If, however, the tribe is absent from the New World Paleogene, the present day paleotropical forms might have been derived from a common European-Asian Paleogene Boreotropical flora, and the South American forms might subsequently have been derived from the African ones.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1-6. Representative seeds of six extant genera of the tribe Monstereae; lateral and ventral views: 1, *Stenospermation* sp., Ecuador, *Madison* 908 (GH), $\times 10$; 2, *Rhaphidophora monticola*, Philippines, *Wenzel* 1160 (GH), $\times 9$; 3, *Epipremnum pinnatum*, Hainan, *Ko* 52235 (GH), $\times 4.5$; 4, *Rhodospatha* sp., Colombia, *Schultes & Cabrera* 18958 (GH), $\times 13$; 5, *Scindapsus officinalis*, Thailand, *Nicolson* 1683 (A), $\times 3$; 6, *Monstera dubia*, Colombia, *Madison* 826 (GH), $\times 2$. (c = chalaza; h = hilum; m = micropyle; r = raphe.)

FIGURE 7. Developmental stages in the growth of the seed of *Monstera dubia*, Colombia, *Madison* 826 (GH), $\times 2$; lateral view.

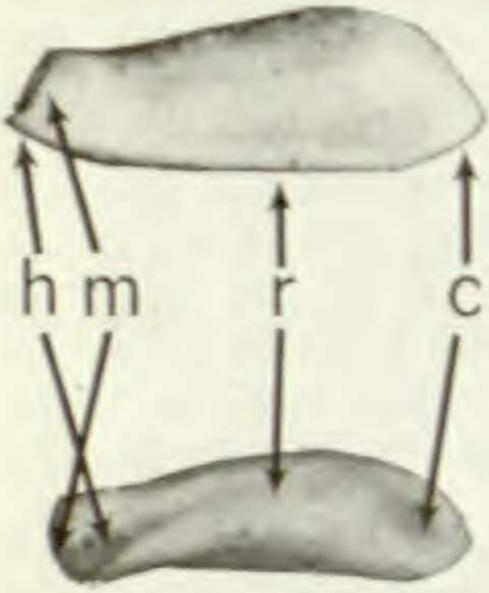
PLATE II

FIGURES 8-34. Seeds of *Stenospermation*, *Rhaphidophora*, *Epipremnum*, *Rhodospatha*, and *Scindapsus*: 8, *Stenospermation* sp. Ecuador, *Madison* 908 (GH), $\times 7.5$; 9, *S. sessile*, Panama, *Duke & Dwyer* 13969 (GH), $\times 7.5$; 10, *Rhaphidophora affinis*, Burma, *Dickason* 5017 (GH), $\times 7.5$; 11, *R. bulusanensi*, Philippines, *Elmer* 16790 (GH), $\times 7.5$; 12, *R. decursiva*, Laos, *Poilane* 20636 (A), $\times 7.5$; 13, *R. grandis*, China, *Wang* 74405 (A), $\times 7.5$; 14, *R. grandis*, New Hebrides, *Kajewski* 830 (A), $\times 7.5$; 15, *R. monticola*, Philippines, *Wenzel* 1160 (GH), $\times 7.5$; 16, *R. reineckeii*, Samoa, *Bryan* 115 (GH), $\times 7.5$; 17, *R. trinerva*, Philippines, *Elmer* 18057 (GH), $\times 7.5$; 18, *R. yunnanensis*, China, *Wang* 74120 (A), $\times 7.5$; 19, *Rhaphidophora* sp., Thailand, *Nicolson* 1655 (A), $\times 7.5$; 20, *Rhaphidophora* sp., Burma, *Dickason* 7823 (A), $\times 7.5$; 21, *Epipremnum amplissimum*, W. New Guinea, *Van Royen* 3123 (A), $\times 3$; 22, *E. elegans*, Solomon Islands, *RSS* 2330 (A), $\times 3$; 23, *E. pinnatum*, Hainan, *Ko* 52235 (GH), $\times 3$; 24, *E. pinnatum*, Solomon Islands, *Brass* 2755 (A), $\times 3$; 25, *Epipremnum* sp., New Guinea, *Hartley* 10259 (A), $\times 3$; 26, *Rhodospatha* sp., Colombia, *Schultes & Cabrera* 18958 (GH), $\times 7.5$; 27, *R. latifolia*, Ecuador, *Madison* 921 (GH), $\times 7.5$; 28, *Scindapsus altissimus*, Papua, *Brass* 8185 (A), $\times 3$; 29, *S. hederaceus*, Sumatra, *Bangham* 1271 (GH), $\times 3$; 30, *S. maclurei*, Thailand, *Nicolson* 1642 (A), $\times 3$; 31, *S. officinalis*, Burma, *Dickason* 5510 (GH), $\times 3$; 32, *S. rupestris*, Borneo, *Clemens* 31094 (A), $\times 3$; 33, *S. subcordatus*, Papua, *Brass* 7269 (A), $\times 3$; 34, *Scindapsus* sp., Papua, *Brass* 13031 (A), $\times 3$.

PLATE III

FIGURES 35-47. Seeds of *Monstera*, *Amydrium*, and *Anadendrum*: 35, *Monstera acuminata*, Mexico, *Madison 1782* (GH), $\times 2$; 36, *M. adansonii* var. *laniata*, Colombia, *Madison 819* (GH), $\times 2$; 37, *M. deliciosa*, Guatemala, *Madison 657* (GH), $\times 2$; 38, *M. dilacerata*, Colombia, *Madison 1213* (GH), $\times 2$; 39, *M. dubia*, Ecuador, *Madison 905* (GH), $\times 2$; 40, *M. lechlerana*, Colombia, *Madison 871* (GH), $\times 2$; 41, *M. membranacea*, Costa Rica, *Madison 738* (GH), $\times 2$; 42, *M. punctulata*, Mexico, *Madison 633* (GH), $\times 2$; 43, *M. siltepecana*, Guatemala, *Madison 661* (GH), $\times 2$; 44, *M. tuberculata*, Costa Rica, *Madison 752* (GH), $\times 2$; 45, *Amydrium magnificum*, Papua, *Brass 25015* (A), $\times 2.5$; 46, *Anadendrum microstachyum*, Java, *Van Steenis 12642* (A), $\times 2.5$; 47, *A. latifolium*, Viet Nam, *Poilane 6384* (A), $\times 2.5$.

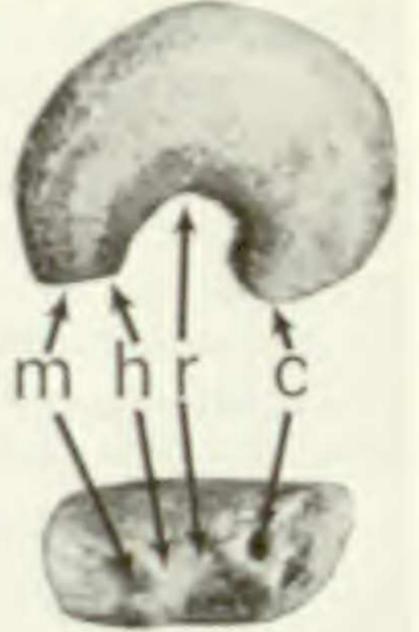
FIGURES 48-51. Araceous fossil seeds from Russian Tertiary deposits: 48, *Epipremnum ornatum* Reid & Chandler. In: A. L. Takhtajan, ed., *Osnovy paleontologii*. [Fundamentals of paleontology.] Vol. 15. Acad. Sci. SSSR. Moscow. 632. fig. 398d. 1963. [Tertiary], $\times 4.2$; 49, *Epipremnum cristatum* Nikitin. In: *Ibid.* fig. 398b. 1963. [Tertiary], $\times 4.2$; 50, *Epipremnum visimense* P. I. Dorofeev, Tretichnye flory Urala. [Tertiary floras of the Ural.] Botanical Institute V. L. Komarova. 35. fig. 2. 1970. [Oligocene], $\times 7.3$; 51, *Epipremnum crassum* C. & E. M. Reid. In: P. I. Dorofeev, O Pliotsenovoi flory Bashkirskogo Predvral'ya. [The Pliocene floras of the Bashkirian foothills of the Urals.] Bask. Fil. Akad. Nauk SSSR. 18. pl. 3, fig. 3. 1960. [Pliocene], $\times 7.5$.



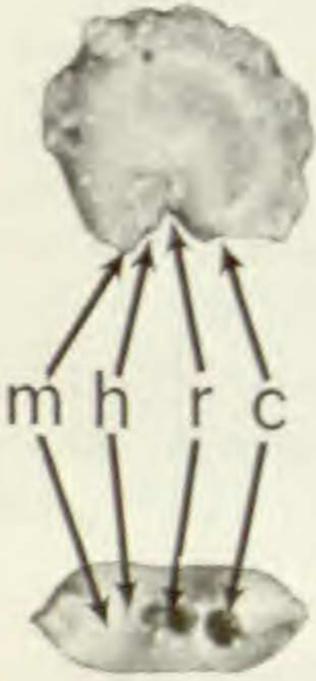
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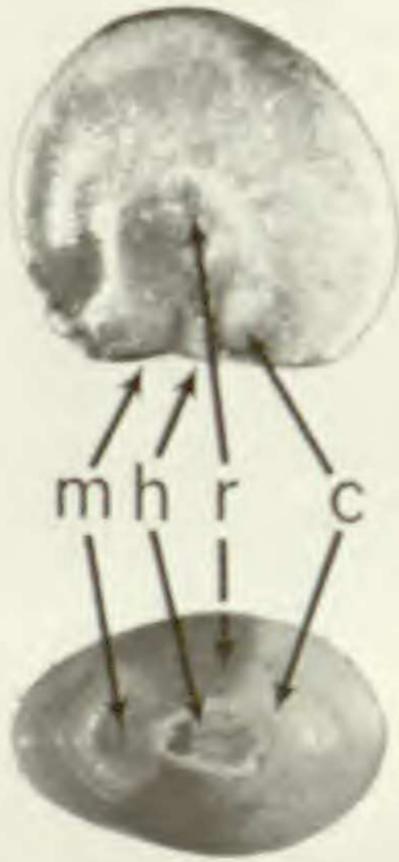
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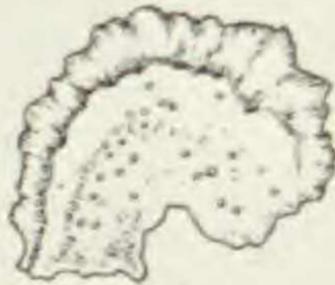
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